In the F_2 generation of all crosses, a complete gradation of reactions between high resistance and full susceptibility was observed, and the mode of inheritance of rust reaction appeared highly complex. Originally the reactions were recorded under six different classes, but quite often plants occurred which could not be clearly defined. As temperature and light conditions play an important part in the development of a particular type of infection, the classification was necessarily arbitrary and it was considered more appropriate to report the data under four classes as shown in Table 3. Considering the highly resistant type of reaction shown by the resistant parents, the plants with an intermediate type of reaction have been grouped with the susceptible class and the (R– and SR) class represents a reaction intermediate between the susceptible and resistant parents.

Mentana was used as the susceptible parent in certain crosses reported in Table 3, but this variety, unlike Federation, is not fully susceptible. The crosses involving Mentana show a deficiency of susceptible plants and an excess of semi-resistant plants: there is, however, no appreciable change in the proportion of fully resistant plants. It appears that the gene or genes responsible for the moderately susceptible reaction of Mentana in conjunction with certain minor genes in the resistant varieties have caused an increase in the proportion of semi-resistant plants with a corresponding reduction in the proportion of susceptible plants.

TABLE 4.

The F_3 Breeding Behaviour at Moderate Temperatures of F_2 Plants of the Cross Federation × Marquillo Representing Different Reaction Types at the Same Temperatures.

F_2 Reactions.	F_3 Reactions.							
	R+	R+ to R R+ to R–	R+ to SR R to SR	R– to SR	R+ to S R to S	R– to S SR to S	S	Total
R+ and R ..	–	22	25	1	2	–	–	50
R– and SR ..	–	2	12	2	9	1	–	26
Int. and S ..	–	–	1	1	64	12	31	109
Total	–	24	38	4	75	13	31	185

Goulden (1930) found that the proportion of resistant plants in the field in crosses between susceptible varieties and Marquillo varied with the susceptible variety used in crosses, but the data in Table 3 do not show any significant variation in the percentage of resistant plants in crosses of this variety with the susceptible parents used here. Slight differences which occur especially at high temperatures in crosses between susceptible varieties and Marquillo, Thatcher and Hochzucht more or less disappear at low temperatures. In addition to minor differences in the genetic constitution of the resistant varieties, the observed variations are likely to occur due to light conditions and minor changes in the temperature.

F_2 plants of the crosses Federation × Marquillo, Federation × Thatcher and Federation × Hochzucht, which had been tested in the glasshouse with race 222AB, were transplanted in the field. The F_3 breeding behaviour of these plants was found against the same race of rust and comparisons of F_2 and F_3 reactions are given in Tables 4, 5 and 6. All the F_3 tests were carried out at moderate temperatures, but only the Federation × Marquillo F_2s had been tested at these temperatures; the F_2s of Federation × Thatcher and Federation × Hochzucht crosses were tested at high temperatures.

The segregating lines in all the three crosses in Tables 4, 5 and 6 did not behave according to any definite pattern, and all sorts of aberrant ratios were indicated. There were lines which showed preponderance of susceptible plants, and there were others in which resistant or semi-resistant plants predominated. There were even lines which contained only one or two resistant or semi-resistant individuals in an average family size of about 20 or 25 plants. It is quite likely that some of the lines which were actually segregating F_3 lines of crosses involving Marquillo, suggested that these may be due to abnormal chromosome behaviour. The cytological studies made by Powers (1932) and Love (1941) show that Marquillo is germinally unstable.

TABLE 5.

The F_3 Breeding Behaviour at Moderate Temperatures of F_2 Plants of the Cross Federation × Thatcher Tested at High Temperatures.

F_2 Reactions.	F_3 Reactions.							
	R+	R+ to R	R+ to SR R to SR	R− to SR	R+ to S R to S	R− to S SR to S	S	Total
R+ and R ..	—	4	—	—	—	—	—	4
R− and SR ..	—	4	19	2	1	—	—	26
Int. and S ..	—	—	7	11	41	7	6	72
Total	—	8	26	13	42	7	6	102

In crosses of Marquillo, Thatcher and Hochzucht with Federation, one important aim was to find lines showing the parental reactions. The results in the preceding tables show that not one F_3 line homozygous for the (R+) type of reaction was recovered in any of the three crosses. The reaction of F_1 plants had shown that resistance was recessive, and in the F_2 generation plants were obtained which were highly resistant like the parents, but the F_3 breeding behaviour of these plants shows that they did not breed true.

TABLE 6.

The F_3 Breeding Behaviour at Moderate Temperatures of F_2 Plants of the Cross Federation × Hochzucht Tested at High Temperatures.

F_2 Reactions.	F_3 Reactions.							
	R+	R+ to R	R+ to SR R to SR	R− to SR	R+ to S R to S	R− to S SR to S	S	Total
R+ and R ..	—	3	1	—	—	—	—	4
R− and SR ..	—	1	19	10	2	2	—	34
Int. and S ..	—	—	5	21	22	28	16	92
Total	—	4	25	31	24	30	16	130

The comparison of F_2 and F_3 reactions at moderate temperatures of the cross Federation × Marquillo shows that most of the resistant plants gave progenies possessing various grades of resistance, and the susceptible plants gave either segregating or susceptible progenies. As it was not possible to provide exactly the same conditions during F_2 and F_3 tests, the minor discrepancies can be expected on the basis of environmental differences. The comparison of F_2 reactions (at high temperatures) and F_3 reactions (moderate temperatures) of the crosses Federation × Thatcher and Federation × Hochzucht reveal more clearly the influence of temperature. Some of the susceptible F_2 plants in both of these crosses gave progenies with various grades of resistance. Almost all the resistant plants gave resistant or partially resistant progenies. A line was actually isolated from the cross Federation × Thatcher, which was homozygous for high resistance at low temperatures, moderate resistance at moderate temperatures and moderate susceptibility at high temperatures.

Seed was available in 105 of the 185 F_3 lines of the cross Federation × Marquillo tested at moderate temperatures (Table 4). These 105 lines were tested against the same race of rust at high temperatures, and the results are compared in Table 7.

Table 7 shows that some of the F_3 lines which were resistant (R+ to R) at moderate temperatures showed segregation at high temperatures (R+ to S or R to S), whilst some of the segregating lines were found to be homozygous susceptible at higher temperatures. A difference in the reaction of F_3 families of a cross between Marquis

TABLE 7.

Comparison of Reactions of 105 F_3 Lines of the Cross Federation × Marquillo at Two Different Temperatures.

Reactions at Moderate Temperatures.	Reactions at High Temperatures.						
	R+ to R	R+ to SR R to SR	R− to SR	R+ to S R to S	R− to S SR to S	S	Total.
R+ to R or R+ to R− ..	2	10	—	7	—	—	19
R+ to SR or R to SR ..	—	14	1	7	1	—	23
R+ to S or R to S ..	—	—	—	18	10	11	39
R− to S or SR to S ..	—	—	—	—	2	3	5
S	—	—	—	—	—	19	19
Total	2	24	1	32	13	33	105

and Marquillo was also observed by Harrington (1931) when tests were made with race 21 at average temperatures of approximately 61° and 70° F. As in the cross Federation × Thatcher, a pure breeding line was isolated from the Federation × Marquillo cross, which showed high resistance to race 222AB at low temperatures, moderate resistance at moderate temperatures and susceptibility at high temperatures. A cross was made between Federation and this line (49.258) to study the mode of inheritance of rust reaction. F_2 data from this cross at low and moderate temperatures are given in Table 8.

TABLE 8.

F_2 Reactions of the Cross Federation × 49·258 against Race 222AB at Moderate and Low Temperatures.

Temperature.	Parents or Cross.	F_2 Reactions.						
		(R+)	(R)	(R−)	(SR)	(Int.)	(S)	Total
Moderate	Parents	—	—	49·258	—	—	Federation	—
,,	Federation × 49·258	—	—	15	22	3	150	190
Low	Parents	49·258	—	—	—	—	Federation	—
	Federation × 49·258	8	30	— 87	—	84	306	515

The results in Table 8 show that even the reaction of the line 49.258 which possesses only part of the resistance complement carried by Marquillo is not simply inherited. At moderate as well as at low temperatures approximately 1/16 of the F_2 plants either equal or approach the reaction of the resistant line and therefore at least two main factors must be assumed to govern the resistant reaction. From these results it can also be inferred that the resistance of Marquillo, Thatcher or Hochzucht must be dependent on several genes and that the action of some of these genes is susceptible to temperature effects.

Random samples of F_3 and F_4 lines of crosses between Federation and each of the resistant varieties were tested against race 222AB at different times during the course of this study, and the results are summarized in Table 9.

The results in Table 9 again show that not one line was pure breeding for the resistant reaction of the parents; there were, however, lines under the class (R+ to R) which closely approached their reaction. Even at high temperatures one out of 91 F_3 lines of the cross Federation × Marquillo belonged to the (R+ to R) class, and this line, though not as resistant as Marquillo, equals the reaction of Thatcher or Hochzucht at that temperature (Table 3). None of the 109 F_3 lines of the cross Federation × Thatcher falls under the class (R+ to R) at high temperatures. The results show that with the rise of temperature there is an increase in the numbers of susceptible lines, and this is accompanied by a reduction in the numbers of resistant lines. The 149 F_4 lines of the cross Federation × Marquillo, and 211 F_4 lines of the cross Federation × Thatcher in Table 9 were tested against race 222AB at low temperatures, and the reactions of these lines at two different temperatures are compared in Tables 10 and 11.

TABLE 9.

Reactions of F_3 and F_4 Lines of Crosses between Federation and Marquillo, Thatcher and Hochzucht.

Temperature.	Cross.	Reactions.						
		R+	R+ to R	R+ to SR R to SR R− to SR	R+ to S R to S	R− to S SR to S	S	Total
High	Federation × Marquillo F_3s	—	1	15	30	23	22	91
Moderate	,, ,, F_4s	—	3	44	41	50	11	149
High	Federation × Thatcher F_3s	—	—	7	10	51	41	109
Moderate	,, ,, F_3s	—	1	42	19	87	30	179
,,	,, ,, F_4s	—	3	51	61	78	18	211
,,	Federation × Hochzucht F_3s	—	—	50	50	84	26	210
,,	,, ,, F_4s	—	1	37	46	28	14	126

TABLE 10.

Comparison of the Reactions of Federation × Marquillo F_4 Lines at Moderate and Low Temperatures.

Reactions at Moderate Temperatures.	Reactions at Low Temperatures.							
	R+	R+ to R	R+ to SR R to SR	R− to SR	R+ to S R to S	R− to S SR to S	S	Total
R+	—	—	—	—	—	—	—	—
R+ to R ..	2	1	—	—	—	—	—	3
R+ to SR or R to SR ..	9	3	15	—	(2)	—	—	29
R− to SR ..	1	3	9	2	—	—	—	15
R+ to S or R to S	—	6	8	—	26	(1)	—	41
R− to S or SR to S	2	1	11	—	23	13	—	50
S	—	—	1	—	2	3	5	11
Total	14	14	44	2	53	17	5	149

Of the F_4 lines of the cross Federation × Marquillo tested at low temperatures (Table 10), 14 were as resistant as Marquillo and another 14 approached this reaction. Though most of these 28 lines showed various grades of resistance at moderate temperatures, some even showed segregation for susceptible individuals. These 28 lines are apparently drawn from all different classes except the susceptible one. Of the 11 lines which were susceptible at moderate temperatures, however, only 5 were susceptible at low temperatures; others showed various grades of resistance or segregation for resistance and susceptibility. These results demonstrate that lines homozygous for high resistance can be obtained more easily at low temperatures.

The 211 F_4 lines of the cross Federation × Thatcher whose reactions at low and moderate temperatures are recorded in Table 11, show a behaviour similar to the Federation × Marquillo cross. The proportion of lines equalling or approaching the reaction of Thatcher at low temperatures is, however, comparatively lower, only 6 lines were classified as (R+) and another 9 lines as (R+ to R).

Tables 10 and 11 show that quite a large number of lines belonged to the same class at the two different temperatures, but in most of these lines a less resistant or a susceptible reaction predominated at lower temperatures. Such differences are not revealed by these tables. A few lines in Tables 10 and 11 recorded in parentheses showed unexpected behaviour, but considering the method of classification and occurrence of abnormal segregation ratios, it should be regarded as a minor discrepancy. It is, however, quite clear from the data in these tables that at the lower temperatures there is a comparatively greater percentage of those lines which approach or equal the reaction of the resistant parent and a smaller percentage of those lines which equal the reaction of the susceptible parent.

TABLE 11.

Comparison of the Reactions of Federation × Thatcher F_4 Lines at Moderate and Low Temperatures.

Reactions at Moderate Temperatures.	Reactions at Low Temperatures.							
	R+	R+ to R	R+ to SR R to SR	R− to SR	R+ to S R to S	R− to S SR to S	S	Total
R+	—	—	—	—	—	—	—	—
R+ to R ..	1	1	(1)	—	—	—	—	3
R+ to SR or R to SR ..	3	5	20	(1)	(1)	—	—	30
R− to SR ..	—	1	9	10	(1)	—	—	21
R+ to S or R to S	2	1	17	1	38	(2)	—	61
R− to S or SR to S	—	1	15	1	25	36	—	78
S	—	—	1	—	2	12	3	18
Total	6	9	63	13	67	50	3	211

Hayes *et al.* (1925) and others who studied the inheritance of Marquillo or Thatcher resistance in the field, concluded that the two or three factors responsible for resistance were complementary in action, but the glasshouse studies reported here show that at least one of the resistance factors has an individual effect of its own which is comparatively weaker and may be susceptible to temperature effect. An examination of Table 8 will show that approximately one-fourth of the total number of plants of the cross Federation × 49·258 tested at low temperatures possess various grades of resistance, and it therefore appears that of the two factors assumed to control the rust reaction, one has some individual effect, and the other gene is strictly of a complementary or modifying nature. Similarly F_3 or F_4 data in crosses of Federation with each of the resistant varieties Marquillo, Thatcher or Hochzucht show that at moderate temperatures approximately 25% or more of the lines show various grades of resistance. Probably the weak effect of a gene is not noticeable in the field. The line 49·258, which was isolated from the cross Federation × Marquillo and which shows a reaction ranging from high resistance at low temperatures to susceptibility at high temperatures, was found to be susceptible in the field where four races of Australian stem rust were prevalent and where Marquillo maintained its high resistance.

It should be emphasized that some of the Federation × Marquillo F_4 lines which appear to be as resistant as Marquillo at low temperatures cannot be regarded as identical with the latter, because such lines do not maintain their high resistance at higher temperatures. So far, out of the few hundred F_3 or F_4 lines of this cross tested at moderate or high temperatures, not a single line bred true for the parental resistance.

In a sample of over 1,000 lines of the cross Garnet × Marquillo, Neatby and Goulden (1930) did not find one line equal to Marquillo in field resistance.

The results reported earlier indicate that it is easier to recover a resistant line of the (R+ to R) type from the cross Federation × Marquillo than from the crosses Federation × Thatcher and Federation × Hochzucht. Table 1 shows that Thatcher and Hochzucht give parallel reactions against all the races, and that these two varieties do not possess as high resistance as Marquillo against a number of races. It appears that these two varieties do not inherit all the resistance genes of Marquillo.

The results on the inheritance of the Marquillo, Thatcher or Hochzucht resistance must be interpreted on a multiple factor basis, some are major factors, whilst others are minor factors which intensify the effect of major genes. Only when all the major and minor genes are present together could a hybrid line maintain the parental reaction at all temperatures. If minor factors for resistance behave as dominant, it will also explain why the resistant F_2 plants do not breed true to their type. It also appears that at least one of the major factors has some individual effect, and one or more factors are susceptible to temperature.

Race Relationship: The reactions of 149 F_4 lines of the Federation × Marquillo cross and 126 F_4 lines of the Federation × Hochzucht cross to race 222AB are recorded in Table 9. These lines gave approximately the same reactions against races 126 and 222BB. Of the 211 F_4 lines of the cross Federation × Thatcher, whose reactions to race 222AB are also given in Table 9, 167 were tested against races 126 and 222BB, and the results showed that these lines behaved in a similar manner against races 222AB, 126 and 222BB. It can be concluded from these studies that the same group of genes in Marquillo, Thatcher or Hochzucht condition resistance to races 222AB, 126 and 222BB.

As shown in Table 2, Marquillo gave a resistant or moderately resistant type of reaction to race 21 at moderate temperatures. The relationship between races 222AB and 21 was also determined by a study of 149 F_4 lines of the cross Federation × Marquillo. A comparison of reactions against the two races showed that all lines which possessed various grades of resistance against race 222AB, showed a comparatively less resistant reaction to race 21; lines susceptible to one race were also susceptible to the other. It appears, therefore, that most of the genes in Marquillo which control its high resistance to race 222AB are responsible for its resistant or moderately resistant reaction against race 21. The line 49·258 selected from the cross Federation × Marquillo was found to be semi-resistant to race 21 at moderate temperatures and susceptible at high temperatures.

Studies with race 21: Thatcher and Hochzucht were immune to race 21. Thatcher inherited its immunity from Kanred which was found by Aamodt (1922) to be dependent on a single dominant factor. Hayes *et al.* (1925) reported that the field resistance of Thatcher derived from Iumillo was inherited independently of the immunity factor.

The inheritance of rust reaction to race 21 was studied in the crosses Federation × Thatcher and Federation × Hochzucht. F_1 seedlings of each of these two crosses were immune to this race. The reactions of F_2 plants at high and low temperatures are given in Table 12, which also includes reactions of 83 F_3 lines of the cross Federation × Hochzucht at high temperatures.

The F_2 data at high temperatures on crosses between Federation and each of the immune parents Thatcher and Hochzucht agree with a 3:1 ratio ($P > 0{\cdot}50$). The reactions were clear-cut and the F_2 segregates were either immune or susceptible. The F_2 data on the same crosses at low temperatures, however, indicate the presence in these varieties of another set of factors for resistance to race 21. If all the plants which are not immune (resistant and susceptible plants) are grouped together the observed data on the crosses Federation × Thatcher and Federation × Hochzucht in Table 12 agree with a 3:1 ratio; the P value respectively lies between 0·10 and 0·20, and 0·30 and 0·50.

The results on 83 F_3 lines of the cross Federation × Hochzucht obtained at high temperatures (Table 12) show that 4 lines gave a reaction ranging from semi-resistance to susceptibility, the rest of the lines were either immune, segregating or susceptible. As semi-resistant reaction does not appear to bear any relationship with the immune reaction, these 4 lines should be combined with the susceptible class. These data agree with a 1:2:1 ratio ($P = 0{\cdot}30–0{\cdot}50$) as expected on the basis of a single factor for immunity.

The breeding behaviour of 105 F_2 plants of the cross Federation × Thatcher, which had been previously tested with race 21 at high temperatures, was determined under similar temperature conditions, and the F_2 and F_3 results are compared in Table 13.

The F_2 plants showing immune type of reaction to race 21 were indistinguishable from the ones which might have escaped infection. Table 13 shows that one of the 79

TABLE 12.

Reactions of Federation × Thatcher F_2 Plants and Federation × Hochzucht F_2 Plants and F_3 Lines against Race 21.

Temperature.	Cross and Generation.	Reactions to Race 21.						
		Immune.	Resistant.		Segregating.		Susceptible.	Total.
			(R)	(SR)	(I to S)	(SR to S)		
High	Federation × Hochzucht F_2	198	—	—	—	—	62	260
,,	,, ,, F_3	16	—	—	41	4	22	83
,,	Federation × Thatcher F_2	132	—	—	—	—	41	173
Low	Federation × Hochzucht F_2	439	6	36	—	—	81	562
,,	Federation × Thatcher F_2	376	4	47	—	—	88	515

plants recorded as immune gave homozygous susceptible progeny. Apparently this plant escaped infection in the F_2 tests. The rest of the immune plants, as expected, gave homozygous immune or segregating progenies. All the susceptible plants except one bred true. The F_3 family from this exceptional susceptible plant showed a range of reaction from semi-resistance to susceptibility. As in the cross Federation × Hochzucht the F_3 data on the Federation × Thatcher cross also agrees with a 1:2:1 ratio ($P = 0{\cdot}95$).

TABLE 13.

The F_3 Breeding Behaviour of Federation × Thatcher F_2 Plants Representing the Immune and Susceptible Reactions.

F_2 Classification.	F_3 Breeding Behaviour.				
	Immune.	Segregating.		Susceptible.	Total.
		(I to S)	(SR to S)		
Immune	27	51	—	1	79
Susceptible	—	—	1	25	26
Total ..	27	51	1	26	105

The F_2 data at low temperatures in Table 12 indicate that both Thatcher and Hochzucht have an additional set of factors for resistance which is completely hypostatic to the immunity factor. It appears, however, that the action of this set of factors is greatly influenced by temperature as there was very little evidence from the F_2 and F_3 data at high temperatures (Tables 12 and 13) for the presence in these varieties of any resistance factor against race 21 except the one controlling immunity.

Thatcher and Hochzucht were immune to race 21 throughout these experiments. As the immunity factor is epistatic, then reactions do not reveal anything about the influence of temperature on the action of a set of factors for resistance present in these varieties. Marquillo was semi-resistant to race 21 at high temperatures, but was highly resistant to the same race at low temperatures (Table 2). It has been found that the same genes in Marquillo which control its high resistance to race 222AB are mainly responsible for the resistance of this variety to race 21. As Thatcher and Hochzucht do not incorporate all the genes for resistance possessed by Marquillo, it is probable that the resistance conferred by the additional set of factors in the former two varieties against race 21 will not be as effective as that of Marquillo. This is apparent from the reaction of Celebration 1374 against race 21. Celebration was developed from the cross Double Cross × Dundee × Dundee (*Agr. Gazette N.S.W.*, 1946), Double Cross being a sister line to the variety Thatcher. Dundee is susceptible to races 222AB and 21.

TABLE 14.

Distribution of Federation × Thatcher and Federation × Hochzucht F_4 Lines for Their Reactions to Races 222AB and 21.

Cross.	Reaction to Race 222AB.	Reaction to Race 21.						
		I	I to SR	I to S	R− to S SR to S	R− to SR R− to Int.	S	Total.
Federation × Thatcher	R+ to R or R+ to SR or R to SR	6	8	7	3	3	—	27
	R− to SR ..	2	1	1	—	5	—	9
	S	2	—	8	—	—	3	13
Total ..	.. ..	10	9	16	3	8	3	49
Federation × Hochzucht	R+ to R or R+ to SR or R to SR	7	7	7	2	6	—	29
	R− to SR ..	3	5	5	—	1	—	14
	S	4	—	7	—	—	3	14
Total ..	.. ..	14	12	19	2	7	3	57

Celebration does not inherit the immunity factor, but it is nearly as resistant as Thatcher to race 222AB. Tests with race 21 showed that this variety was moderately susceptible at high temperatures, and gave a resistant reaction at moderate temperatures. Evidently Celebration and probably Thatcher and Hochzucht do not possess all of the resistance genes which confer a semi-resistant reaction on Marquillo against race 21 at high temperatures.

F_4 lines of the crosses Federation × Thatcher and Federation × Hochzucht which were either susceptible or showed various grades of resistance against race 222AB at moderate temperatures were tested against race 21 at the same temperatures. Table 14 presents a comparison of reaction against the two races.

The data in Table 14, though not very extensive, are quite revealing. The results show that the immunity of Thatcher and Hochzucht to race 21 is inherited independently of their resistance to race 222AB. Some of the F_4 lines which were susceptible to race 222AB are homozygous immune to race 21. It is also apparent from the preceding table that there are other genes both in Thatcher and Hochzucht producing a moderately resistant or semi-resistant reaction against race 21, as lines were obtained breeding pure for this reaction. Probably these genes would give higher resistance at low temperatures. As in the case of Marquillo, these genes in Thatcher and Hochzucht for partial resistance to race 21 appear to belong to the same group of genes upon which depends the resistance of each of these varieties to race 222AB.

Genetic Relationship between Marquillo, Thatcher and Hochzucht.—Data on F_1, F_2 and F_3 generations of diallel crosses among the three varieties are presented in Table 15.

Marquillo × *Thatcher.*—The F_1 seedlings of this cross were highly resistant to race 222AB. As the resistance of the two parents in crosses with Federation was recessive, the results indicate that the same loci in Marquillo and Thatcher condition resistance. No susceptible segregate was observed in the F_2 and F_3 populations of this cross, and these results confirm the indications obtained from the behaviour of F_1 plants.

It will be observed from the table that of the 943 F_2 plants of the cross of Thatcher × Marquillo two were not as highly resistant as Marquillo. The occurrence of such plants can probably be explained on the basis of germinal instability of Marquillo (Love, 1941) as plants showing lower resistance have sometimes been found even in the parent lines. It is also possible that the occurrence of less resistant plants may be due

TABLE 15.

F_1, F_2 and F_3 Reactions of Diallel Crosses among Marquillo, Thatcher and Hochzucht against Races 222AB and 21.

Cross and Generation.	Race.	Reactions.					
		Immune.	Resistant.			Sus-ceptible.	Total.
			(R+)	(R)	(R−)		
Marquillo × Thatcher F_1 ..	222AB	—	6	—	—	—	6
,, ,, F_1 ..	21	5	—	—	—	—	5
,, ,, F_2 ..	222AB	—	941	— 2 —		—	943
,, ,, F_2 ..	21	635	—	— 180 —		1 (Int.)	816
,, ,, F_3 ..	222AB	—	166	—	—	—	166
Marquillo × Hochzucht F_1 ..	222AB	—	6	—	—	—	6
,, ,, F_1 ..	21	6	—	—	—	—	6
,, ,, F_2 ..	222AB	—	747	— 7 —		—	754
Thatcher × Hochzucht F_1 ..	222AB	—	6	—	—	—	6
,, ,, F_1 ..	21	8	—	—	—	—	8
,, ,, F_2 ..	222AB	—	936	— 21 —		—	957
,, ,, F_2 ..	21	1480	—	—	—	—	1480
,, ,, F_3 ..	222AB	—	145	—	—	—	145
,, ,, F_3 ..	21	123	—	—	—	—	123

to the difference among the two varieties in minor genes controlling rust reaction. Single plants showing less resistance were also encountered in a few F_3 families, but as all the other plants in such families were showing high resistance, these were classed as highly resistant (R+).

It was earlier concluded that the same genes in Marquillo, and probably Thatcher, which confer resistance against race 222AB were also operating against race 21. These genes are, however, not as effective in producing resistance against race 21 as they are against race 222AB. There was evidence that the genes for resistance in Thatcher, in the absence of the immunity factor, can produce a moderately resistant reaction against race 21 at moderate temperatures. These genes will probably show high resistance to this race at low temperatures. It can, therefore, be inferred that no susceptible plant should be obtained in the cross Marquillo × Thatcher at least at low temperatures when tested against race 21, and approximately three-quarters of the F_2 plants should be immune.

257 F_2 plants of the cross Marquillo × Thatcher were tested with race 21. The results were obtained at low temperatures, and are not included in the table. 199 plants were immune and 58 showed a highly resistant reaction, and the agreement of the observed data to a 3:1 ratio is satisfactory ($P = 0{\cdot}30–0{\cdot}50$). Another sample of 816 plants whose reactions are recorded in Table 15 (635 I, 180 R to R–, 1 Int.) was tested at moderate temperatures. The immune and non-immune plants agree with a 3:1 ratio with a P value of only 0·05–0·10. The poor agreement is due to the excess of immune plants which probably include some escapes. A plant giving an intermediate type of reaction also

occurred in the F_2 population, and it would probably be possible to get even susceptible plants at high temperatures.

It can be concluded that the major genes for resistance to races 222AB and 21 in Marquillo and Thatcher are allelomorphic and the factor for immunity against race 21 present in Thatcher is inherited independently of the genes giving resistance.

Thatcher × Hochzucht.—Against race 222AB, this cross showed the same behaviour as the Marquillo × Thatcher cross. As indicated in Table 15, F_1 plants were highly resistant and no susceptible segregate was obtained in the F_2 and F_3 generations. The tests carried out with race 21 showed that all the F_2 plants and F_3 lines were immune. It appears that Thatcher and Hochzucht have similar genetic backgrounds, both for high resistance to race 222AB and for immunity to race 21.

Marquillo × Hochzucht.—As expected, the results in Table 15 show that most of the genes for resistance in Marquillo and Hochzucht are at the same loci.

Relationship of Marquillo, Thatcher and Hochzucht to Kenya 744 and Kenya 117A 1347.—It has been shown (Athwal and Watson, 1954) that the seedling resistance of Kenya 744 and Kenya 117A to four Australian rusts is dependent upon single factors which are allelomorphic and probably identical. These two varieties are also resistant to race 21 and further work has revealed that the same factor both in Kenya 744 and Kenya 117A confers resistance against races 222AB and 21. The reactions of a selected sample of 102 F_4 lines of the cross Federation × Kenya 744 (43 Resistant, 40 susceptible, 19 segregating) and 70 F_4 lines of the cross Federation × Kenya 117A (30 Resistant, 25 susceptible, 15 segregating) were found to be the same against these two races. As expected, no plant susceptible to race 21 was observed in an F_2 population of 665 individuals of the cross Kenya 744 × Kenya 117A.

The present studies indicate that major genes for high resistance to race 222AB in Marquillo, Thatcher and Hochzucht are allelomorphic and that most of these are also responsible for a less resistant reaction against race 21. The results also show that the immunity of Thatcher and Hochzucht to race 21 is conditioned at the same locus. For the sake of convenience, the major genes for resistance in Marquillo, Thatcher and Hochzucht will be referred to as the resistance factors and a single factor for immunity in the latter two varieties as the immunity factor. It was the purpose of the following studies to examine the relationship of the locus conditioning Kenya resistance against races 222AB and 21 to the resistance genes and the immunity factor. The following crosses were studied: Marquillo × Kenya 744; Marquillo × Kenya 117A; Thatcher × Kenya 744; Thatcher × Kenya 117A; Hochzucht × Kenya 744; Hochzucht × Kenya 117A.

On the basis of previous results these six crosses should show the same behaviour against race 222AB and the required information could have been obtained by a study of any one cross. As the crosses had, however, been made in the absence of present knowledge and the material was available, it was considered appropriate to collect data on all of them.

The reaction of Kenya varieties to races 222AB and 21 was R–. For the reactions of other parents see Table 2 (Moderate temperatures).

The data in Table 16 show that, excepting one plant in the cross Marquillo × Kenya 744 which appeared to be susceptible, no other segregate susceptible to race 222AB was obtained in an F_2 population of several hundred plants of these crosses. This single susceptible plant was transplanted in the field, and its F_3 progeny, when tested with the same race of rust, gave a reaction ranging from a semi-resistant to intermediate type. The F_3 breeding behaviour of a sample representing the small proportion of F_2 plants with intermediate type of reaction observed in these crosses proved that genotypically they resembled closely semi-resistant F_2 plants. The F_3 data in Table 17 show that these crosses do not yield any segregating or susceptible line. It appears, therefore, that the locus conditioning Kenya resistance is strongly linked with one of the major genes in Marquillo, Thatcher or Hochzucht. This major gene is apparently capable of producing at least a semi-resistant reaction when present alone, and this fact has already been indicated in the inheritance studies with these varieties.

The reactions of F_1 seedlings of crosses of Kenya varieties with Thatcher and Hochzucht against race 21 (Table 16) show that immunity is epistatic to the Kenya resistance. Of the 819 F_2 plants of the cross Thatcher × Kenya 117A tested against the same race, 622 were immune, 196 R– and SR and 1 Intermediate. The observed frequency of the immune and non-immune plants agree with a 3:1 ratio ($P = 0{\cdot}50–0{\cdot}70$).

TABLE 16.

Reactions to Race 222AB and 21 of F_1 and F_2 Populations of Crosses of Kenya Varieties with Marquillo, Thatcher and Hochzucht.

Cross and Generation.	Race.	Reactions.					
		Immune.	Resistant.		Inter-mediate.	Sus-ceptible.	Total.
			(R+) and (R)	(R−) and (SR)			
Marquillo × Kenya 744 F_1 ..	222AB	—	—	14	—	—	14
,, ,, ,, F_2 ..	222AB	—	322	983	15	1	1321
Marquillo × Kenya 117A F_1 ..	222AB	—	—	11	—	—	11
,, ,, ,, F_2 ..	222AB	—	— 821	—	11	—	832
Thatcher × Kenya 744 F_1 ..	222AB	—	—	7	—	—	7
,, ,, ,, F_1 ..	21	8	—	—	—	—	8
,, ,, ,, F_2 ..	222AB	—	251	— 788	—	—	1039
Thatcher × Kenya 117A F_1 ..	222AB	—	—	3	—	—	3
,, ,, ,, F_1 ..	21	5	—	—	—	—	5
,, ,, ,, F_2 ..	222AB	—	74	250	1	—	325
,, ,, ,, F_2 ..	21	622	—	196	1	—	819
Hochzucht × Kenya 744 F_1 ..	222AB	—	—	4	—	—	4
,, ,, ,, F_1 ..	21	4	—	—	—	—	4
,, ,, ,, F_2 ..	222AB	—	153	519	3	—	675
Hochzucht × Kenya 117A F_1	222AB	—	—	2	—	—	2
,, ,, ,, F_1	21	4	—	—	—	—	4
,, ,, ,, F_2	222AB	—	77	409	—	—	486

As the resistance factors in Thatcher and Hochzucht against race 222AB appear to be also operative against race 21 at the moderate temperatures prevailing during this test, no fully susceptible segregate is normally expected. 118 F_2 families of the three-way cross (Thatcher × Kenya 117A) × Federation were also tested against race 21. The reactions were complicated by the operation of the resistance factors but there was definite evidence that 6 of these families did not yield any segregate with resistance like that of Kenya 117A. It appears that the immunity factor is not in any way related to the Kenya factor for resistance.

TABLE 17.

Reactions to Race 222AB of F_3 Lines of Crosses of Kenya Varieties with Marquillo and Thatcher. (Reactions of Parents are the same as in Table 16.)

Cross.	F_3 Reactions to Race 222AB.					
		Resistant.			Sus-ceptible.	Total.
	(R+ to R)	(R− to SR)	(R+ to SR)	(R− to Int.)		
Marquillo × Kenya 744 ..	17	43	102	1	—	163
Marquillo × Kenya 117A ..	20	— 67	—	—	—	87
Thatcher × Kenya 744 ..	18	80	151	—	—	249

DISCUSSION.

The results obtained by Hayes *et al.* (1925), Neatby and Goulden (1930), Ausemus (1934), Pan (1940), Platt *et al.* (1941), Swenson *et al.* (1947), and Koo and Ausemus (1951) show that the field resistance of Marquillo or Thatcher is dependent on at least two, three or more factors. Neatby and Goulden (1930) reported that when Marquillo was crossed with (Marquis × Kanred B_{2-5}) the operation of three or more factors was indicated, but when Garnet or Reward were used as susceptible parents, many factors appeared to be involved, and Neatby (1931, 1933) later found that Marquillo and Thatcher do not possess any additional factor for mature plant resistance, except the ones which are operative in the seedling stage. The results obtained from the present studies in the glasshouse indicate that Marquillo, Thatcher and Hochzucht present a very similar mode of inheritance against race 222AB, and most of the resistance factors in these varieties are allelomorphic and probably identical. The segregation in crosses between a susceptible and each of the resistant varieties is influenced by temperature, and results can be best explained on a multiple factor hypothesis. It was of some significance to isolate a line from the cross Federation × Marquillo which was resistant at low temperatures, and susceptible at high temperatures.

Lines homozygous for partial resistance were obtained in all crosses between Federation and Marquillo, Thatcher or Hochzucht but not one line incorporated the full resistance of the parents. This fact probably throws some light on the difficulty encountered in transferring the full resistance of Iumillo to Marquillo. It has also been seen that Thatcher and Hochzucht do not possess all the minor genes for resistance in Marquillo as a greater percentage of resistant lines was recovered in crosses involving the latter variety. The results are in agreement with those of Neatby and Goulden (1930), who suggested that Marquillo possesses one or two minor factors for field resistance in addition to those concerned in the Double Cross resistance. Powers (1932) and Love (1941) found that Marquillo shows abnormal chromosome behaviour and it is possible that Iumillo chromosomes bearing some of the resistance factors do not show complete homology with the *vulgare* chromosomes, and tend to be eliminated during meiosis. It seems, however, quite easy to transfer partial resistance from Marquillo, Thatcher or Hochzucht, as there appears to be present at least one factor in these varieties which can singly produce a resistant reaction. The presence of such a factor is of some importance in relation to the factor controlling Kenya resistance as the two appear to be strongly linked. Probably it will not be possible to combine all the major genes for resistance in Marquillo with the single factor in Kenya varieties, but it may not be difficult to couple partial resistance from the former source with the full resistance of Kenya 744 or Kenya 117A.

The results on the inheritance of Marquillo resistance at low and moderate temperatures to race 222AB show some similarity with those obtained by Harrington (1931). In the cross Marquis × Marquillo, he found a reversal in the genetic ratios when F_3 seedling families were tested to race 21 at an average temperature of about 70° F. and 61° F. Only 1/64 of the F_3 families were resistant like Marquillo at the higher temperature, while only 1/64 were found to be susceptible like Marquis at the lower temperature. Harrington explained these results by assuming that the action of three dominant genes for susceptibility present in Marquis was greatly curtailed or reduced at the lower temperature. The results obtained here show that 3 of the 149 F_4 lines of the cross Federation × Marquillo approached the resistant reaction of Marquillo at moderate temperatures, while at low temperature some highly resistant lines were obtained, and only 5 lines were homozygous for susceptibility. It was suggested that this difference in the segregation is due to the presence in Marquillo of some genes which are influenced by temperature. The resistance of Marquillo to race 21 has been found to depend mainly on the same genes which confer resistance against race 222AB.

It has been seen that Hochzucht and Thatcher appear to have the same genetic constitution both with respect to resistance and immunity to certain races of *Puccinia graminis tritici*. As the factor for immunity is not effective against Australian rusts, Thatcher and Hochzucht do not add to the genetic diversity for resistance possessed by Marquillo. Because Marquillo possesses some minor genes for resistance which are not present in Thatcher or Hochzucht, it appears more appropriate to use the former for incorporating resistance to rust in this country. It has already been found that Marquillo is slightly more resistant to Australian rusts than Thatcher and Hochzucht at higher temperatures, and it is comparatively easy to secure a resistant line in crosses of a susceptible variety with Marquillo. The reactions in Table 1 also show that Marquillo possesses higher resistance than Thatcher and Hochzucht against certain other races of stem rust.

Acknowledgements.

Our thanks are due to our colleague, Dr. E. P. Baker, who has helped from time to time when necessary. We acknowledge also the help from the laboratory assistant staff, and financial help from the Rural Bank of New South Wales.

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THE NYMPH OF *EUSCHÖNGASTIA SMITHI* (WOMERSLEY, 1939) (ACARINA, TROMBICULIDAE).

By Robert Domrow, Queensland Institute of Medical Research, Brisbane.

(Ten Text-figures.)

[Read 29th June, 1955.]

Synopsis.

The nymph of *Euschöngastia smithi* (Wom.) is described, being the second of this genus to be correlated with its larva in Australia. The nymph emerged fifteen to nineteen days after detachment. A key to the three known nymphs of Australian *Euschöngastia* is given.

The second Australian-bred nymph of the genus *Euschöngastia* Ewing, *E. smithi* (Wom.), is described in this note. The other, *E. perameles* (Wom.), was described by the author in an earlier paper (Domrow, 1955).

On 18.i.55 a specimen of *Rattus assimilis* Gould from Mt. Glorious, south-east Queensland, was examined. Fairly numerous chiggers were found in the ears, both in small groups and singly. These were removed with a needle. Half were mounted and identified as *E. smithi*, except for one specimen of *E. derricki* (Wom.). Twelve larvae were set up in tubes after the method described by Audy and Nadchatram (1954), and fifteen to nineteen days later eight nymphs emerged. The active period lasted up to five days. After the eight nymphs had emerged some remaining larvae, which apparently were not fully engorged, were still active, but died later. The larvae were trapped by the smallest droplets of moisture, while the nymphs could move over the moist glass surface with ease.

Euschöngastia smithi (Womersley, 1939).

Types: Six morphotype nymphs in collection of Queensland Institute of Medical Research, Brisbane, and one each at South Australian Museum, Adelaide, and Institute for Medical Research, Kuala Lumpur. All nymphs are accompanied by correlated larval pelts and were bred from engorged larvae taken from inside the ears of *Rattus assimilis* Gould, Mt. Glorious, south-east Queensland, 18.i.55.

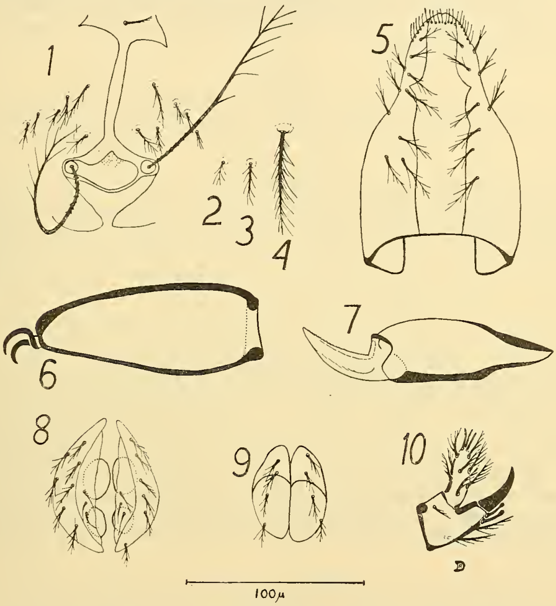
Description of Nymph.

Body: Mean idiosomal length 568μ (range 470μ to 607μ), breadth across propodosoma 269μ (233μ to 296μ), across hysterosoma 288μ (249μ to 311μ); well marked constriction at level of posterior pair of coxae; pale straw colour in life. Genital area oval (Text-fig. 8), 76·8μ long, with two pairs of genital suckers; anterior sucker 18·8μ, posterior sucker 14·9μ long. Genital plates with six or seven pairs of ciliated setae; inner genitalia constantly with three pairs of setae, which may be simple or bifurcate apically; two anal plates (Text-fig. 9) 49·6μ long, rather more heavily chitinized anteriorly, normally with four pairs of ciliated setae. The genitalia are placed just behind coxae IV, and the anal plates are separated by slightly less than their own length from the genitalia.

Gnathosoma: Chelicerae (Text-fig. 7) with fine teeth dorsally; blade 52μ long. Hypostome (Text-fig. 5) blunt anteriorly, with about twenty simple setae; base of gnathosoma with nine or ten pairs of ciliated setae, which are somewhat slenderer than body setae.

Palpi (Text-fig. 10) 5-segmented, similar in shape to *E. perameles*; tibial claw 28·6μ long. Femur with three or four dorsal and one external ciliated setae; genu with six or seven dorso-lateral ciliated setae; tibia with five external and one internal ciliated setae; with two internal, dorsal, sub-apical, spatulate accessory spines in addition to strong apical spine; tarsus with eight internal and one external ciliated setae, one external sensory rod, and three apical simple setae.

Legs: Leg I largest, leg IV longer than legs II and III, which are almost equal; all 7-segmented; coxae I with precoxal plates fused medially as in *E. perameles*. All tarsi with two strong claws (Text-fig. 6). Coxae I and II and III and IV in two distinct groups, only coxae I being fused. Tarsus I 118μ long, 53μ high; tibia I 86μ long, tarsus II 71μ long, tibia II 47μ long. Tarsus I without preapical dorsal process (Text-fig. 6); *E. perameles* also has no such process.



Text-figs. 1-10.—*Euschöngastia smithi* (Wom., 1939). Nymph. 1, Scutum. 2, Anterior dorsal seta. 3, Mid-dorsal seta. 4, Posterior dorsal seta. 5, Hypostome and basal part of gnathosoma in ventral view. 6, Tarsus I in lateral view. 7, Chelicera in lateral view. 8, Genitalia. 9, Anal plates. 10, Palpal tibia and tarsus, interior aspect.

Scutum (Text-fig. 1): Sensillary area roughly diamond-shaped, with anterior part punctate between sensillary bases. Tectum with anterior margin indistinct, and with single weakly ciliated tectal seta. Median saddle present on sensillary area, connecting sensillary bases. Chitinization around sensillary bases sometimes asymmetrical. Posterior apodeme with irregular sides, with sinuous lines diverging laterally at the apex as in *E. perameles*. Sensillae filiform, of fairly uniform thickness, but slightly thicker medially, with basal barbules, and ciliations to 20μ distally. Eyes absent. Parascutal setae one on each side with five to seven adjacent setae. The scutal standard data are given in Table 1, after Audy (1953).

Setation: Dorsal body setae (Text-figs. 2 to 4) increasing in length posteriorly from 14·2μ just behind scutum to 60·3μ at posterior margin of hysterosoma. All setae are set on platelets as in *E. perameles*, but the posterior setae are also on small tubercles on the platelet. In *E. perameles* the setation is much more uniform. The ventral setae are similar, and strongly ciliated like those on the dorsum. The setation of the legs is in general similar to *E. perameles*. Precoxal plates with three or four setae each.

Coxa I with twelve to eighteen, coxa II with eight or nine, coxa III with eight to fifteen, and coxa IV with nine to fifteen ciliated setae.

Taxonomic Notes.

Like *E. perameles*, the nymph of *E. smithi* also runs readily to caption 10 in Womersley's key (1952, p. 366), and may be separated from *E. mutabilis* by its longer sensillae and the nature of the dorsal hairs, and from *E. nadchatrami* by its much smaller size, short crista, and the presence of precoxal plates. The larvae of all three species are quite distinct. *E. smithi* and *E. perameles* appear to be much more closely related to one another, both in larval and nymphal stages, than to either of the last two species. The following key is offered to separate the three known nymphs of Australian *Euschöngastia* Ewing.

TABLE 1.

Standard Data (in Micra) of Scutum of E. smithi.

	CTL	ASL	SB	ASL/SB	PSL	PAD	TS	SS	SENS
	71·4	82·1	48·2	1·70	14·3	32·1	15·0	27·5	123·2
	75·0	85·7	—	—	12·5	35·7	16·1	28·6	117·8
	71·4	85·7	42·8	2·00	14·3	32·1	14·3	26·8	117·8
	71·4	83·9	41·1	2·04	—	—	—	28·6	—
	67·8	80·3	41·1	1·95	16·0	30·3	16·1	28·6	117·8
Means..	71·4	83·5	43·3	1·92	14·3	32·6	15·4	28·0	119·2

Key to nymphs of Australian Euschöngastia.

1. Precoxal plates absent, sensillae slightly clavate .... *E. indica* (Hirst).
   Precoxal plates present, sensillae filiform .... 2.
2. Dorsal setae relatively uniform in length, 23-32μ long; precoxal plates with about seven setae each; anal plates with about six pairs of setae; no simple inner genital setae; a larger species, 720 to 780μ long; known only from *Isoodon obesulus* .... *E. perameles* (Wom.).
   Dorsal setae increasing in length posteriorly, 14 to 60μ long; precoxal plates with three or four setae each; anal plates with four pairs of setae; three pairs of simple inner genital setae present; a smaller species, 470-600μ long; known only from *Rattus assimilis* .... *E. smithi* (Wom.).

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A NEW SPECIES OF *ECHINONYSSUS* HIRST, 1925, FROM QUEENSLAND (ACARINA : LIPONYSSINAE).

By Robert Domrow, Queensland Institute of Medical Research, Brisbane.

(Two Text-figures.)

[Read 29th June, 1955.]

Synopsis.

Echinonyssus validipes, n. sp., from the rat-kangaroo, *Potorous tridactylus*, from Queensland is described and discussed. A key to the two known species is given.

Recently two rat-kangaroos (*Potorous tridactylus* Kerr) from south-east Queensland were examined for ectoparasites. They yielded some very interesting mites belonging to a new species of *Echinonyssus* Hirst, 1925 (Liponyssinae). The other species of the genus (*E. nasutus* Hirst, 1925) is recorded only as a single specimen from the Oriental tree-shrew, *Tupaia picta*, from Sarawak.

Echinonyssus validipes, n. sp.

Types: The holotype female, allotype male, paratype males, and morphotype nymphs are in the collection of the Queensland Institute of Medical Research, Brisbane. Paratypes of both sexes are also in the South Australian Museum, Adelaide. The type series was collected on two rat-kangaroos, *Potorous tridactylus* Kerr, Mt. Nebo, south-east Queensland, 24.ix.54 and 17.i.55.

Female (Text-fig. 1).

A small, pale, weakly chitinized species; idiosoma length 660μ, breadth 455μ. *Dorsal shield* not completely covering dorsum, slightly constricted medially; twenty pairs of very small setae on dorsal shield; thirteen pairs of somewhat longer setae on dorsal marginal cuticle. *Peritreme* very short, situated dorsally above coxa III; stigma slightly swollen.

Venter. Sternal shield large, narrower anteriorly, and slightly convex posteriorly; three pairs of fine sternal setae and two pairs of punctate pores present. Genito-ventral shield drop-shaped, with two pairs of short setae; genital operculum large, extending forward well past centre of sternal shield, and with numerous very fine longitudinal striations (not shown in illustration). Anal shield elongate, with heavier chitinizations laterally; all three anal setae weak. Ventral cuticle striated, with about twelve pairs of simple setae. Tritosternum present, with weakly ciliated lacinae.

Legs. All coxae with heavily chitinized spurs; anterior ventral margin of coxa II with large hook, which curves ventrally and caudally, being used to grasp the fur of the host. Smaller, retrorse spurs present ventrally on tibia and genu I, and on tarsi, tibiae, and genua III and IV. Femora I and II with long seta dorsally, while femur I also has a chitinized process with a small, apical seta.

Chelicerae weakly chitinized, long, and slender, 213μ; two digits about equally developed, straight, blade-like, and without teeth; blades 66μ long and up to 7·1μ wide.

Male (Text-fig. 2).

Most specimens are approximately equal in size to female (670μ long, 443μ wide), but odd ones are somewhat larger; more heavily chitinized, and with much stronger legs. *Dorsal shield* larger, and not constricted medially; with 31 pairs of setae, of which eleven anterior marginal and three discal pairs are weak, five posterior pairs are strong, and twelve discal pairs are in the form of stout, blunt spines. Dorsal marginal cuticle with about seven pairs of simple setae. *Peritreme* as in female.